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PLANT ADAPTATION IN THE GREAT BASIN AND COLORADO PLATEAU

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ABSTRACT—Adaptive features of plants of the Great Basin are reviewed. The combination of cold winters and an arid to semiarid precipitation regime results in the distinguishing features of the vegetation in the Great Basin and Colorado Plateau. The primary effects of these climatic features arise from how they structure the hydrologic regime. Water is the most limiting factor to plant growth, and water is most reliably available in the early spring after winter recharge of soil moisture. This factor determines many characteristics of root morphology, growth phenology of roots and shoots, and photosynthetic physiology. Since winters are typically cold enough to suppress growth, and drought limits growth during the summer, the cool temperatures characteristic of the peak growing season are the second most important climatic factor influencing plant habit and performance. The combination of several distinct stress periods, including low-temperature stress in winter and spring and high-temperature stress combined with drought in summer, appears to have limited plant habit to a greater degree than found in the warm deserts to the south. Nonetheless, cool growing conditions and a more reliable spring growing season result in higher water-use efficiency and productivity in the vegetation of the cold desert than in warm deserts with equivalent total rainfall amounts. Edaphic factors are also important in structuring communities in these regions, and halophytic communities dominate many landscapes. These halophytic communities of the cold desert share more species in common with warm deserts than do the nonsaline communities. The Colorado Plateau differs from the Great Basin in having greater amounts of summer rainfall, in some regions less predictable rainfall, sandier soils, and streams which drain into river systems rather than closed basins and salt playas. One result of these climatic and edaphic differences is a more important summer growing season on the Colorado Plateau and a somewhat greater diversification of plant habit, phenology, and physiology.

Key words: cold desert, plant adaptation, water stress, phenology, salinity, Great Basin, Colorado Plateau.

Several features arising from climate and geology impose severe limitations on plant growth and activity in the Great Basin and Colorado Plateau. The climate is distinctly continental with cold winters and warm, often dry summers. Annual precipitation levels are low in the basins, ranging from 100 to 300 mm (4–12 inches), and typically increasing with elevation to 500 mm (20 inches) or more in the montane zones. Precipitation levels are lowest along the southwestern boundary of the Great Basin in Nevada and increase both to the north and east, and to the southeast moving into the Colorado Plateau (Fig. 1, Table 1). The fraction of annual precipitation during the hot summer months (June–September) varies considerably, from 10–20% in northern Nevada to 30–40% along the boundary of the Cold and Mojave deserts in southwestern Nevada and southern Utah, and 35–50% throughout much of the Colorado Plateau. Winter precipitation falls primarily as snow in the Great Basin and higher elevations

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TABLE 1. Selected climatic data for low-elevation sites in different regions of the Great Basin, Mojave Desert, and Colorado Plateau. Values are based on averages for the U.S. Weather Bureau stations indicated. The three divisions of the year presented here reflect ecologically relevant units, but are unequal in length. The five months of October–February represent a period of temperature-imposed plant dormancy and winter recharge of soil moisture. The spring months of March–May represent the potential growing period at cool temperatures immediately following winter recharge. The summer and early fall from June through September represent a potential warm growing season in areas with sufficient summer rain or access to other moisture sources.

Region	Map # (Fig. 1)	Weather station	Elevation (m)	Total precipitation				Mean temperature			
				Annual (mm)	Oct–Feb (%)	Mar–May (%)	Jun–Sep (%)	Annual (°C)	Oct–Feb (°C)	Mar–May (°C)	Jun–Sep (°C)
Northern	1	Fort Bidwell	1370	402	63	24	13	9.0	3.0	8.0	17.3
Great Basin	2	Reno	1340	182	61	24	15	9.5	3.3	8.4	18.0
	3	Elko	1547	230	52	29	19	7.6	0.1	7.1	17.5
	4	Snowville	1390	300	43	33	24	7.4	0.7	6.2	18.4
Southern	5	Sarcobatus	1225	85	45	22	33	13.5	6.4	12.5	23.1
Great Basin	6	Caliente	1342	226	47	24	29	11.7	4.1	11.2	21.5
	7	Fillmore	1573	369	44	34	22	11.0	3.0	10.0	21.7
Mojave Desert	8	Trona	517	102	70	19	11	19.0	11.3	18.4	29.0
	9	Beaverdam	570	169	50	23	28	18.3	11.0	16.9	28.6
Colorado	10	Hanksville	1313	132	36	19	45	11.4	2.1	11.5	22.8
Plateau	11	Grand Junction	1478	211	39	25	36	11.3	2.4	10.9	22.9
	12	Blanding	1841	336	48	19	33	9.7	2.1	8.7	19.9
	13	Tuba City	1504	157	38	21	41	12.6	4.8	12.0	22.8
	14	Chaco Canyon	1867	220	35	20	45	10.3	2.6	9.4	20.6

of the Colorado Plateau, which is thought to be a critical feature ensuring soil moisture recharge and a reliable spring growing season (West 1983, Caldwell 1985, Dobrowolski et al. 1990). During the winter period, precipitation is generally in excess of potential evaporation, but low temperatures do not permit growth or photosynthesis, and exposed plants may experience shoot desiccation due to dry winds and frozen soils (Nelson and Tiernan 1983). Strong winds can also cause major redistributions of the snowpack, sometimes reversing the expected increase in precipitation with elevation and having important consequences to plant distributions (Branson et al. 1976, Sturges 1977, West and Caldwell 1983). The important growing season is the cool spring when the soil profile is recharged from winter precipitation; growth is usually curtailed by drying soils coupled with high temperatures in early or mid-summer. A clear picture of this climatic regime is essential to any discussion of plant adaptations in the region.

A second major feature affecting plant performance is the prevalence of saline soils caused by the combination of low precipitation and the internal drainage typical of the Great Basin. In this paper we address the salient morphological, physiological, and phenological specializations of native plant species as they relate to survival and growth under the constraints of these potentially stressful limitations. We emphasize (1) edaphic factors, particularly soil salinity and texture, and (2) the climatic regime ensuring a fairly dependable, deep spring recharge of soil moisture despite the overall aridity, as factors molding plant adaptations and producing the unique aspects of the regional plants and vegetation. The majority of the Great Basin lies at moderately high elevations (4000 ft and above), and it is occupied by cold desert plant communities. Reference to "the Great Basin" and its environment in this paper will refer to this high-elevation region as distinct from that corner of the Mojave Desert that occupies the southwestern corner of the Great Basin geographic unit (Fig. 1). Our emphasis will be placed on these cold desert shrub communities in both the Great Basin and the Colorado Plateau ranging from the topographic low points of the saline playas or canyon bottoms up to the pinyon-juniper woodland. The lower-elevation, warmer,

Great Basin

Mojave

Colorado Plateau

Fig. 1. Distribution of the major desert vegetation zones in the Great Basin and Colorado Plateau. Numbers indicate locations of climate stations for which data are presented in Table 1. Most of the Mojave Desert indicated is geologically part of the Great Basin, but, due to its lower elevation and warmer temperatures, it is climatically distinct from the rest of the region.

and drier Mojave Desert portion of the Great Basin will be considered primarily as a point of comparison, and for more thorough coverage of that region we recommend the reviews by Ehleringer (1985), MacMahon (1988), and Smith and Nowak (1990). For the higher montane and alpine zones of the desert mountain ranges, the reader is referred to reviews by Vasek and Thorne (1977) and Smith and Knapp (1990). We are indebted in our own coverage of the cold desert to other recent reviews, including Caldwell (1974, 1985), West (1988), Dobrowolski et al. (1990), and Smith and Nowak (1990).

The Great Basin and the Colorado Plateau share important climatic features such as overall aridity, frequent summer droughts, and continental winters; yet they differ in other equally important features. Temperatures on the Colorado Plateau are similar to equivalent elevations in the southern Great Basin, but summer precipitation is substantially greater on the Colorado Plateau (Table 1). Soils and drainage patterns also differ in crucial ways. The highlands of the Colorado Plateau generally drain into the Colorado River system. In many areas extensive exposure of marine shales from the Chinle, Mancos, and Morrison Brushy-Basin formations weather into soils that restrict plant diversity and total cover due to high concentrations of $NaSO_4$, and the formation of clays that do not allow water infiltration (Potter et al. 1985). In other areas massive sandstone outcrops often dominate the landscape. Shrubs and trees may root through very shallow rocky soils into natural joints and cracks in the substratum. Deeper soils are generally aeolian deposits forming sands or sandy loams. In contrast, high elevations of the Great Basin drain into closed valleys and evaporative sinks. This results in greater average salinity in the lowland soils of the Great Basin, with NaCl being the most common salt (Flowers 1934), and a more extensive development of halophytic or salt-tolerant vegetation. Soils tend to be deep, especially at lower elevations, and vary in texture from clay to sandy loams. Summer-active species with different photosynthetic pathways, such as C_4 grasses and CAM succulents, are poorly represented in much of the Great Basin, but the combination of increased summer rain, sandier soils, and milder winters at the lower elevations of the Colorado Plateau has resulted in a greater expression of phenological diversity.

The interactions of edaphic factors and climate are complex and often subtle in their effects on plant performance. Furthermore, plant distributions are rarely determined by a single factor throughout their geographic range, even though a single factor may appear to control distribution in the context of a local ecosystem. Species-specific characteristics generally do not impart a narrow requirement for a specific environment, but rather a unique set of "ranges of tolerance" to a large array of environmental parameters. In different environmental contexts, different tolerances may be more limiting, both abiotic and biotic interactions may be altered, and the same set of species may sort out in different spacial patterns. A further consequence of this is that a local combination of species, which we might refer to as a Great Basin plant community, represents a region of overlap in the geographically more extensive

and generally unique distributions of each component species. In fact, the distributions of species commonly associated in the same Great Basin community may be strongly contrasting outside the Great Basin. This is an essential point in attempting to discuss plant adaptations with the implication of cause and effect, because few species discussed will have a strict and exclusive relationship with the environment of interest. Unless we can show local, ecotypic differentiation in the traits discussed, we need to take a broad view of the relationship between environment and plant characters. In a few instances, a small number of edaphic factors and plant characters, such as tolerance of very high salinity in soil with shallow groundwater, seem to be of overriding importance. In most cases we need to ask, what are the common elements of climate over the diverse ranges of all these species? One such common element, which will be emphasized throughout this review, is the importance of reliable winter recharge of soil moisture in an arid to semiarid climate. By identifying such common elements and focusing on them, we do not fully describe the autecology of any species, but we attempt a cogent treatment of plant adaptations to the Great Basin environment, and an explanation of the unique features of its plant communities.

CLIMATE, EDAPHIC FACTORS, AND PLANT DISTRIBUTION PATTERNS

Typical zonation patterns observed in species distributions around playas (the saline flats at the bottom of closed-drainage basins) are quite dramatic, reflecting an overriding effect of salinity on plant distribution in the Great Basin. Moving out from the basin center is a gradient of decreasing soil salinity often correlated with progressively coarser-textured soils. Along this gradient there are conspicuous species replacements, often resulting in concentric zones of contrasting vegetation (Flowers 1934, Vest 1962). In the lowest topographic zone, saline groundwater may be very near the surface. Soils are very saline, fine textured, and subject to occasional flooding and anoxic conditions. In this environment the combination of available moisture with other potentially stressful soil characteristics seems to be more important than climatic factors of temperature or seasonal rainfall patterns. Species found here, such as desert saltgrass (*Distichlis spicata*), pickleweeds

(*Allenrolfia occidentalis* and *Salicornia* spp.), and greasewood (*Sarcobatus vermiculatus*), may themselves show zonation due to degrees of tolerance. They tend to occur in close proximity, however, on the edges of salt playas, saline flats with shallow water tables, and near saline seeps over a wide range of elevations, temperatures, and seasonal rainfall patterns in both the Great Basin and southern warm deserts (MacMahon 1988). This relative independence of distribution from prevailing climate is a special characteristic of strongly halophytic plant communities throughout the world and reflects the overriding importance of such extreme edaphic conditions. Species found on better-drained, moderately saline soils, where groundwater is not found within the rooting zone, include winterfat (*Ceratoides lanata*) and shadscale (*Atriplex confertifolia*). These species are, in turn, replaced at higher elevations and on moister, nonsaline soils by big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* sp.), bitterbrush (*Purshia* sp.), and spiny hopsage (*Grayia spinosa*). Shadscale is often found in areas where soils are notably saline in the lower half of the rooting zone, but not in the upper soil layers. Such a tolerance of moderately saline soils seems to control its distribution around playas, especially in the wetter, eastern portion of the Great Basin (western Utah) and lower elevations in the warm Mojave Desert. In the more arid regions of western and central Nevada, however, the shadscale community occurs widely on nonsaline slopes lower in elevation, warmer, and drier than those dominated by big sagebrush. These higher bands of shadscale have been variously interpreted in terms of aridity tolerance and climate (Billings 1949) or an association with limestone-derived calcareous soils (Beatley 1975). The latter author points out that even on nonsaline soils percent cover in the shadscale community is lower than expected for the level of precipitation, and argues that this indicates stress from edaphic factors. Thus, shadscale distribution is most correlated with salinity tolerance in some regions and other edaphic and climatic tolerances in other regions.

Where the higher elevations of the Great Basin come in contact with the lower-elevation, generally drier, and warmer Mojave Desert region, communities dominated by creosote (*Larrea tridentata*) replace sagebrush communities on nonsaline slopes and bajadas.

Shadscale can be found both on saline soils at very low elevations in the Mojave and as a transitional band at high elevations between creosote and sagebrush. Elements of the cold desert shrub communities, adapted to continental winters and a cool spring growing season, can be found throughout the winter-rain-dominated Mojave Desert region as a high-elevation band on arid mountain ranges. They also extend to the southeast at high elevations into the strongly bimodal precipitation regime of the Colorado Plateau, and northward at low elevations into Idaho, Washington, and even British Columbia. Moving up from bajadas of the southern warm deserts, there appears to be no suitable combination of temperature and precipitation at any elevation to support floristic elements of the cold desert. As precipitation increases with altitude, zones with equivalent total precipitation do not yet have cold winters and are occupied by warm desert shrub communities grading into chaparral composed of unrelated taxa. Higher elevations with cold winters have sufficient precipitation to support forests. Other elements common in shadscale and mixed-shrub communities of the Great Basin, such as winterfat and budsage (*Artemisia spinosa*), are often found outside the Great Basin in cold-winter but largely summer-rainfall grasslands.

From these patterns of community distribution within the Great Basin and Colorado Plateau, and also from a consideration of the more extensive ranges and affinities of the component species, we can isolate a few key features of the environment that are largely responsible for the unique plant features seen in the Great Basin. The most obvious features are related to the patterns of soil salinity and texture generated by the overall aridity combined with either internal drainage basins or the in situ weathering of specific rock types. The most important climatic variables are slightly more subtle. There is clearly not a requirement for exclusively winter rainfall, but there is a requirement for at least a substantial portion of the annual rainfall to come during a continental winter. This permits winter *accumulation* of precipitation to a *greater depth* in the soil profile than will occur in response to less predictable summer replenishment of drying soil moisture reserves. Under an overall arid climate, winter recharge maintains a predictably favorable and dominant spring growing season even in many areas of strongly bimodal rainfall. Most of the physiological, morphologi-

cal, and phenological traits found in the dominant shrubs reflect the primary importance of such a cool spring growing season.

PHOTOSYNTHESIS

PHOTOSYNTHETIC PATHWAYS.—The process of photosynthesis in plants relies on the acquisition of CO_2 from the atmosphere, which, when coupled with solar energy, is transformed into organic molecules to make sugars and provide for plant growth. In moist climates plant communities often achieve closed canopies and 100% cover of the ground surface. Under these conditions competition for light may be among the most important plant-plant interactions. In the deserts total plant cover is much less than 100%, and in the Great Basin closer to 25%. Photosynthesis is not greatly limited by available light, but rather by water, mineral nutrients needed to synthesize enzymes and maintain metabolism, and maximum canopy leaf-area development.

Three biochemical pathways of photosynthesis have been described in plants that differ in the first chemical reactions associated with the capture of CO_2 from the atmosphere. The most common and most fundamental of these pathways is referred to as the C_3 pathway because the first product of photosynthesis is a 3-carbon molecule. The other two pathways, C_4 and CAM, are basically modifications of the primary C_3 pathway (Osmond et al. 1982). The C_4 pathway (first product is a 4-carbon molecule) is a morphological and biochemical arrangement that overcomes photorespiration, a process that results in reduced photosynthetic rates in C_3 plants. The C_4 pathway can confer a much higher temperature optimum for photosynthesis and a greater water-use efficiency. As water-use efficiency is the ratio of photosynthetic carbon gain to transpirational water loss, C_4 plants have a metabolic advantage in hot, dry environments when soil moisture is available. In grasslands C_4 grasses become dominant at low elevations and low latitudes where annual temperatures are warmest. In interpreting plant distribution in deserts, the seasonal pattern of rainfall usually restricts the periods of plant growth, and the temperature during the rainy season is thus more important than mean annual temperature. The C_4 pathway is often associated with summer-active species and also with plants of saline soils. While C_3 grasses predominate in

most of the Great Basin, C_4 grasses become increasingly important as summer rain increases to the south, and especially on the Colorado Plateau. Halophytic plants are often C_4, such as saltbush (*Atriplex* spp.) and saltgrass (*Distichlis* spp.), and this may give the plants a competitive advantage from increased water-use efficiency on saline soils.

The third photosynthetic pathway is CAM photosynthesis (Crassulacean Acid Metabolism). CAM plants open their stomata at night, capture CO_2 and store it as malate in the cell vacuole, and keep their stomata closed during the day (Osmond et al. 1982). The CO_2 is then released from the vacuole and used for photosynthesis the following day. Because the stomata are open only at night when it is cool, water loss associated with CAM photosynthesis is greatly reduced. This pathway is often found in succulents such as cacti and agave, and, although CAM plants are present in the Great Basin, they are a relatively minor component of the vegetation.

Photosynthetic rates of plants, like most metabolic processes, show a strong temperature dependence. Usually, photosynthetic rates are reduced at low temperatures because of the temperature dependence of enzyme-catalyzed reaction rates, increase with temperature until some maximum value (which defines the "temperature optimum"), and then decrease again at higher temperatures. The temperature optima and maximum photosynthetic rates of plants show considerable variation, and they generally reflect the growing conditions of their natural environments.

PHOTOSYNTHETIC ADAPTATION.—In the spring the photosynthetic temperature optima of the dominant shrub species are typically as low as 15 C (40 F) (Caldwell 1985), corresponding to the prevailing environmental temperatures (midday maxima generally less than 20 C). As ambient temperatures rise 10–15 C in the summer, there is an upward shift of only 5–10 C in the photosynthetic temperature optima of most shrubs, coupled with a slower decline of photosynthesis at high temperatures. The maximum photosynthetic rates measured in most Great Basin shrubs under either natural or irrigated conditions range from 14 to 19 μmol CO_2 m^{-2} s^{-1} (DePuit and Caldwell 1975, Caldwell et al. 1977, Evans 1990). These rates are quite modest compared to the high maxima of 25 to 45 μmol CO_2 m^{-2} s^{-1} observed in many warm-desert species adapted to rapid growth at higher temperatures (Ehleringer and Björkman 1978, Mooney et al. 1978, Comstock and Ehleringer 1984, 1988, Ehleringer 1985). This presumably reflects the specialization of these Great Basin shrubs towards utilization of the cool spring growing season. Positive photosynthetic rates are maintained even when leaf temperatures are near freezing, which permits photosynthetic activity to begin in the very early spring (DePuit and Caldwell 1973, Caldwell 1985).

Unusually high maximum photosynthetic rates of 46 μmol CO_2 m^{-2} s^{-1} have been reported for one irrigated Great Basin shrub, rabbitbrush (*Chrysothamnus nauseosus*) (Davis et al. 1985). This species is also unusual in having a deep tap root that often taps groundwater, unusually high levels of summer leaf retention (Branson et al. 1976), and continued photosynthetic activity throughout the summer drought (Donovan and Ehleringer 1991). All of these characters suggest greater photosynthetic activity during the warm summer months than is found in most Great Basin shrub species.

SHOOT ACTIVITY AND PHENOLOGY.—Generally speaking, there is a distinct drought in early summer (June–July) in the Great Basin Cold Desert, the Mojave Desert, and the Sonoran Desert. All of these deserts have a substantial winter precipitation season, but they differ in the importance of the summer and early fall rainy season (July–October) in supporting a distinctive period of plant growth and activity (MacMahon 1988). The relationship between climate and plant growing season is complex and includes total rainfall, seasonal distribution of rainfall, and predictability of rainfall in different seasons as important variables. Furthermore, in very arid areas the seasonality of temperatures may be as important as that of rainfall. In the Great Basin, cold winters allow the moisture from low levels of precipitation to accumulate in the soil for spring use, while hot summer temperatures cause rapid evaporation from plants and soil. High temperatures can prevent wetting of the soil profile beyond a few centimeters depth in response to summer rain, even when summer rain accounts for a large fraction of the annual total (Caldwell et al. 1977). As total annual rainfall decreases, the relative importance of the cool spring growing season increases as the only potential growing period in which available soil moisture approaches the evaporative demand (Thornthwaite 1948, Comstock and Ehleringer 1992). Finally, reliability

of moisture is important to perennials, and as average total precipitation decreases, the variance between years increases (Ehleringer 1985); variability of annual precipitation is discussed in more detail later in the section on annuals and life-history diversity. Summer rain is more likely to be concentrated in a few high-intensity storms that may not happen every year at a given site and may cause more runoff when they do occur. The ability of moisture from winter rain to accumulate over several months greatly enhances its reliability as a moisture resource. Thus, most plants in the Great Basin have their primary growing season in the spring and early summer. Some species achieve an evergreen canopy by rooting deeply, but few species occur that specialize on growth in the hot summer season (Branson et al. 1976, Caldwell et al. 1977, Everett et al. 1980). Ehleringer et al. (1991) measured the ability of common perennial species in the Colorado Plateau to use moisture from summer convection storms. They observed that less than half of the water uptake by woody perennial species was from surface soil layers saturated by summer rains. Prevalence of summer-active species increases along the border between higher basins and the southeast Mojave Desert where summer rain is more extensive, and especially on the Colorado Plateau where summer rain is greatest. Summer temperatures are also lower on the Colorado Plateau than in the eastern Mojave (Table 1), allowing more effective use of the moisture.

Most phenology studies, especially from the more northern areas, emphasize the directional, sequential nature of the phenological phases (Branson et al. 1976, Sauer and Uresk 1976, Cambell and Harris 1977, West and Gastro 1978, Pitt and Wikeem 1990). A single period of spring vegetative growth is usually followed by a single period of flowering and reproductive growth. Many species produce a distinct cohort of ephemeral spring leaves and a later cohort of evergreen leaves (Daubenmire 1975, Miller and Schultz 1987). For most species, multiple growth episodes associated with intermittent spring and summer rainfall events do not occur. In years with unusually heavy August and September rains, a distinct second period of vegetative growth may occur in some species (West and Gastro 1978). Climatic variations from year to year do not change the primary importance of spring growth or the order of phenological events. In particular years, they may cause

expansion or contraction of vegetative phases and even the omission of reproductive phases.

Most species initiate growth in early spring (March) when maximum daytime temperatures are 5–15 C and while nighttime temperatures are still freezing. Delayed initiation of spring growth is generally associated with greater summer activity and may be related to an evergreen habit, a phreatophytic habit, or occupation of habitats with greater summer moisture availability from regional rainfall patterns, runoff, or groundwater. Higher-than-average winter and spring precipitation tends to prolong vegetative growth and delay reproductive growth till later in the summer (Sauer and Uresk 1976, Cambell and Harris 1977). Strong vegetative dormancy may be displayed in mid-summer (Everett et al. 1980, Evans 1990), although root growth (Hodgkinson et al. 1978) and increased reproduction (West and Gastro 1978, Evans, Black, and Link 1991) may still occur in response to rain at that time. In years with below-average spring and summer precipitation, leaf senescence is accelerated and flowering may not occur in many species.

The time taken to complete the full annual growth cycle including both vegetative and reproductive stages is strongly related to rooting depth in most of these communities, with deep-rooted species prolonging activity further into the summer drought (Pitt and Wikeem 1990). The exact timing of flowering and fruit set shows considerable variation among different shrub species. Some, especially those that are drought-deciduous, flower in late spring and early summer just prior to or concurrent with the onset of summer drought. Many evergreen shrub species begin flowering in midsummer (*Artemisia*) or in the fall (*Gutierrezia* and *Chrysothamnus*). These late-flowering species generally do not appear to utilize stored reserves for flowering, but rely on current photosynthesis during this least favorable period. In the case of *Artemisia tridentata*, it has been shown that carbohydrates used to fill fruits are derived exclusively from the inflorescences themselves, while photosynthate from vegetative branches presumably continues to support root growth. Summer rain during this time period does not promote vegetative shoot growth but does increase water use by and the ultimate size of inflorescences (Evans 1990). Evans, Black, and Link (1991) have argued that this pattern of flowering, based on residual deep soil moisture

and the unreliable summer rains, may contribute to competitive dominance within these communities. The more favorable and much more reliable spring growing season is used for vegetative growth and competitive exploitation of the soil volume, while reproductive growth is delayed until the less favorable season, and may be successful only in years with adequate summer precipitation.

Most grasses in the northern part of the Great Basin utilize the C_3 pathway and begin growth very early in the spring. These species complete fruit maturation by early or midsummer, often becoming at least partially dormant thereafter. On the Colorado Plateau, with much greater amounts of summer precipitation, there is a large increase in species number and cover by C_4 grasses such as bluestem (*Andropogon*) and grama (*Bouteloua*), especially at warmer, lower elevations and on deep sandy soils. Many of these species occur in mixed stands with the C_3 species but delay initiation of growth until May or June; they can be considered summer-active rather than spring-active. In contrast, some C_4 grasses such as sand dropseed (*Sporobolus cryptandrus*), galleta grass (*Hilaria jamesiii*), and three-awn (*Aristida purpurea*) are widespread in the Great Basin where summer rain is only moderate in long-term averages and very inconsistent year to year. Spring growth of these widespread species tends to be slightly or moderately delayed compared to co-occurring C_3 grasses, but they are still able to complete all phenological stages based on the spring moisture recharge. They show a greater ability than the C_3 species to respond to late spring and summer rain with renewed growth (Everett et al. 1980), however, which compensates in some years for their later development. Other C_4 grasses in the Great Basin may be associated with seeps, streamsides, or salt-marshes, and show a summer activity pattern. C_4 shrubs such as saltbush (*Atriplex*) show similar, spring-active growth patterns to the C_3 shrubs, but may show slightly greater tolerance of summer drought (Caldwell et al. 1977).

Phenology in the Mojave Desert shows both similarities and strong contrasts to the Great Basin. Although rainfall is largely bimodal in the eastern Mojave, absolute amounts are very low. The summer is so hot that little growth normally occurs at that time unless more than 25 mm (1 inch) comes in a single storm (Ackerman et al. 1980). Fall and winter precipitation is the most important in promoting good spring growth of perennials (Beatley 1974). Comstock et al. (1988), looking at one year's growth in 19 Mojave species, described an important cohort of twigs initiated during the winter period that accounted for most vegetative growth during the following spring. Although new leaves were produced in response to summer rain, summer growth in many of the species was largely a further ramification of spring-initiated floral branches. In most species summer growth made little contribution to perennial stems. Despite the preferred winter-spring orientation of many shrubs, winter recharge is much less effective and reliable in the Mojave Desert than in the Great Basin. Due to warmer temperatures, winter dormancy may be less complete, but vigorous growth rarely occurs until temperatures rise further in the early spring. Rapid growth may be triggered by rising spring temperatures or may be delayed until major spring rains provide sufficient moisture (Beatley 1974, Ackerman et al. 1980). Furthermore, a shallower soil moisture recharge often results in fluctuating plant water status and multiple episodes of growth and flowering during the spring and early fall. Some Great Basin species that also occur in the Mojave, such as winterfat and shadscale, commonly show multiple growth and reproductive episodes per year under that climate (Ackerman et al. 1980) but not in the Great Basin (West and Gastro 1978). The degree to which this difference is due entirely to environmental differences as opposed to ecotypic differentiation does not appear to have been studied.

WATER RELATIONS

ADAPTATION TO LIMITED WATER.—Stomatal pores provide the pathway by which atmospheric CO_2 diffuses into the leaf replacing the CO_2 incorporated into sugar molecules during photosynthesis. Because water vapor is present at very high concentrations inside the leaf, opening stomata to capture CO_2 inevitably results in transpirational water loss from the plant; thus, leaf water content is decreased, resulting in a decrease in plant water potential (Ψ). Thus, plant water status, transpiration, and acquisition of water from the soils have a tremendous impact on photosynthetic rates and overall plant growth.

Many soils in the Great Basin are fine tex-tured, which has both advantages and disadvan-tages for plant growth. Infiltration of water is slower in fine-textured soils, increasing the like-lihood of runoff and reduced spring recharge, especially on steeper slopes. They are also more prone to water-logging and anoxic conditions. The deep root systems of Great Basin shrubs are very sensitive to anoxia, and this can be a strong determining factor in species distributions (Lunt et al. 1973, Groeneveld and Crowley 1988). Unusually wet years may even cause root dieback, especially at depth. Once water enters the soil profile, the extremely high surface areas of fine-textured soils with high clay and silt content give them a much higher water-holding capacity than that found in sandy, coarse-tex-tured soils. Much of this water is tightly bound to the enormous surface area of the small particles, however, and is released only at very negative matric potentials. Plants must be able to tolerate low tissue water potentials to make use of it.

As soil water is depleted during summer, plants reduce water consumption by closing sto-mata (DePuit and Caldwell 1975, Cambell and Harris 1977, Caldwell 1985, Miller 1988) and reducing total canopy leaf area to a minimum (Branson et al. 1976). Evergreen species shed only a portion of the total canopy, however, maintaining the youngest leaf cohorts through-out the drought (Miller and Schulz 1987). Although physiological activity is greatly reduced by water stress, evergreens such as sagebrush can still have positive photosynthetic rates at leaf water potentials as low as −50 bars (Evans 1990) and may survive even greater levels of stress. In contrast, crop plants can rarely survive prolonged Ψ of less than −15 bars. Remaining functional at low water potentials requires the concentration of solutes in the cell sap, and this appears to be accomplished by several mechanisms. In many mesic species, increases in organic solutes may account for most of the change in osmotic potential. In other species, and especially those that experience very low leaf water potentials, a large fraction of the solutes is acquired by the uptake of inor-ganic ions such as $K+$ (Wyn Jones and Gorham 1986). High concentrations of inorganic ions may be toxic to enzyme metabolism, however, and they are widely thought to be sequestered largely in the central vacuole, which accounts for 90% of the total cell volume, even though

much of the evidence for this is quite indirect. Nonetheless, the osmotic potential of the cyto-plasm must also be balanced or suffer dehydra-tion. The cytoplasmic solutes must have the special property of lowering the osmotic poten-tial of the cell sap without disrupting enzyme function or cellular metabolism, and are hence termed "compatible" solutes (Wyn Jones and Gorham 1986). The use of specific molecules shows considerable variation across species apparently due to both species-specific varia-tions in cell metabolism and taxonomic relation-ships. Some frequently encountered molecules thought to function in this manner include amino acids such as proline and also special sugar-alcohols. Some plants appear to generate low osmotic potentials by actively manufactur-ing larger quantities of dissolved organic mole-cules per cell in response to water stress, a process referred to as "osmotic adjustment." This process may be costly, however, requiring the investment of large amounts of materials (new solutes) at a time when water stress is largely inhibiting photosynthetic activity. An alternative method seems to involve dramatic changes in cell water volume. Several desert species have been observed to reduce cell water volume by as much as 80% without wilting when subjected to extremely low soil water potentials (Moore et al. 1972, Meinzer et al. 1988, Evans et al. 1991). This allowed the leaf cells to have sufficiently low osmotic potentials for water uptake even though solute content per cell was actually reduced. Although total solutes per leaf (and presumably per cell) decreased, the rela-tive concentrations of specific solutes changed (Evans et al. 1991) such that "compatible" solutes made larger contributions to the osmotic potential under stress. Thus, tolerance of low leaf water potentials was achieved by a combi-nation of anatomical and physiological special-izations. The anatomical mechanisms involved in this magnitude of volume reduction and the implied cell elasticity have not been studied, but the process has been shown to be fully reversible.

Soil texture is also an important factor in determining the ability of plant communities in a cold-winter climate to respond to summer rain. In areas with moderate levels of precipita-tion, sandy soils, because of their low water-holding capacity, usually hold a sparser, more drought-adapted vegetation than finer-textured ones. In warm, arid areas, however, what has been called the "reverse texture" effect results

in the more lush vegetation occurring in the coarse-textured soils. This occurs because the high water-holding capacity of fine-textured soils allows them to hold all the moisture derived from a single rainfall event in the uppermost layers of the soil profile, where it is highly subject to direct evaporation from the soil. The same amount of rainfall entering a sandy soil, precisely because of its low water-holding capacity, will penetrate to a much greater depth. It is also less likely to return to the drying surface by capillary action. Less of the rain will evaporate from the soil surface, and a greater fraction of it will await extraction and use by plants. This inverse-texture effect further restricts the effectiveness of summer rains in the fine soils of the Great Basin. The effect is less operative in respect to winter precipitation in the Great Basin, however, because of the gradual recharge of the soil profile to considerable depth under conditions where surface evaporation is minimized by cold temperatures. The combination of much sandier soils and greater amounts of summer rainfall in the region of the Colorado Plateau is largely responsible for the major floristic and ecological differences between the two regions. At lower elevations on the southeast edge of the plateau, shrub-dominated desert scrub may be replaced by grassland dominated by a mix of spring-active C_3 and summer-active C_4 species.

ROOTING DEPTH, MORPHOLOGY, AND PHENOLOGY —One of the unique and ecologically most important features of the Great Basin shrub communities is not apparent to aboveground observers. This is the investment of the vast majority of plant resources in the growth, maintenance, and turnover of an enormous root system. The dominant shrubs of the Great Basin usually root to the full depth of the winter-spring soil moisture recharge. Depending on soil texture, slope aspect, and elevation, this is generally between 1.0 and 3.0 m (Dobrowolski et al. 1990). Although this represents a wide range of absolute depths, many of the qualitative patterns of rooting behavior are similar on most of these sites. Ratios of root:shoot standing biomass range from 4 to 7, and estimates of root:shoot annual carbon investment are as high as 3.5. Most of the shrubs have a flexible, generalized root system with development of both deep taproots and laterals near the surface. Moreover, it is the category of fine roots < 3.0 mm in diameter that constitutes 50–95% (Cald-

well et al. 1977, Sturges 1977) of the total root biomass. The very large annual root investments, therefore, are not primarily related to large storage compartments, but to the turnover of fine roots and root respiration necessary for the acquisition of water and mineral nutrients.

The fine root network thoroughly permeates the soil volume. Root densities are generally quite high throughout the upper 0.5 meters of the profile, but depth of maximum root development varies with depth of spring soil-moisture recharge, species, and lateral distance from the trunk or crown. A particularly high density in the first 0.1 m may often occur, especially immediately under the shrub canopy (Branson 1976, Caldwell et al. 1977, Dobrowolski et al. 1990). Alternatively, maximal density may occur at depths between 0.2 m and 0.5 m (Sturges 1980), and sometimes a second zone of high root density is reported at depths of 0.8 m (Daubenmire 1975) to 1.5 m (Reynolds and Fraley 1989). Regardless of the precise depth of maximum rooting, shrub root density is usually high throughout the upper 0.5 m and then tapers off, but may continue at reduced densities to much greater depth. The radius of lateral spread is usually much greater for roots (1–2 m) than for canopies (0.1–0.5 m). Percent plant cover aboveground is often in the neighborhood of 25% with 75% bare ground, but belowground the interspaces are filled with roots throughout the profile, and root systems of adjacent plants will overlap. The perennial grasses that are potentially co-dominant with shrubs in many of these communities, such as wheatgrass (*Agropyron* sp.), wildrye (*Elymus* sp.), squirreltail (*Sitanion histrix*), Indian ricegrass (*Oryzopsis hymenoides*), and galleta grass (*Hilaria jamesii*), generally have somewhat shallower root systems than the shrubs (Branson et al. 1976, Reynolds and Fraley 1989, Dobrowolski et al. 1990). Root densities of grasses are often as high as or higher than those of shrubs in the upper 0.5 m but taper off more rapidly such that shrubs usually have greater density at depth and greater maximum penetration.

The moisture resource supporting the greatest amount of plant growth is usually the water stored in the soil profile during the winter. This profile usually has a positive balance, with more water being added by precipitation than is withdrawn by evapotranspiration between October and March. As temperatures warm in March, evergreen species may begin drawing on this

moisture reserve, and most species begin active growth in March or April. Due to both plant water use and soil-surface evaporation, soil moisture is depleted first in the shallow soil layers. As the upper layers dry, plants withdraw moisture from successively deeper soil layers, a process that continues in evergreen species throughout the summer until soil moisture is depleted throughout the profile. This progression of seasonal water use beginning in superficial layers and proceeding to deeper soil layers is facilitated by the pattern of fine root growth, which shows a similar spatial and temporal pattern (Fernandez and Caldwell 1975, Caldwell 1976). Root growth generally precedes shoot growth in the early spring and continues throughout the summer in evergreen species, which may appear quiescent aboveground. In annual budgets of undisturbed communities, soil moisture withdrawal almost always approaches measured precipitation over a wide range of annual fluctuations in total precipitation, and very little moisture is lost to runoff or deep drainage beneath the rooting zone (Daubenmire 1975, Caldwell et al. 1977, Cambell and Harris 1977, Sturges 1977). Calculations of the portion of evapotranspiration actually used by plants in transpiration are quite high for a desert environment with low percent cover; they range from 50 to 75% (Caldwell et al. 1977, Cambell and Harris 1977, Sturges 1977).

Competition for soil moisture is not necessarily limited to any single season. Plant water stress is highest in late summer, and survival is most likely to be influenced at this time, especially if one plant can deplete residual soil moisture below the tolerance range of another. This has been shown in several cases with regard to seedling establishment (Harris 1977, DeLucia and Schlesinger 1990, Reichenberger and Pyke 1990). Growth and productivity are more likely to be affected in the spring and early summer growing season. This is because most of the year's water resource is already stored in the soil in early spring, and all plants are drawing on a dwindling reserve which ultimately determines growing season length. Competitive ability is often found to be associated with an ability to begin using the limiting water resource earlier in the spring (Eissenstat and Caldwell 1988, Miller 1988), but spatial partitioning is also important. Competition may be most intense in shallower soil layers because grasses and drought-deciduous shrubs, which are active only in the spring, are shallower rooted, and lateral root spread of the evergreen species is greatest in the shallower soil layers. The more dominant perennials usually use more water over the whole season by tapping deeper soil layers (Cline et al. 1977, Sturges 1980) and are characterized by higher water-use efficiencies (DeLucia and Schlesinger 1990, Smedley et al. 1991).

Shrubs appear to be better than grasses at withdrawing water from deep soil layers for several reasons. In shallow soils underlain by fractured or porous bedrock, the flexible, multiple taproot structure of a shrub root system may be better suited than the more diffuse, fibrous root system of grasses for following chinks and cleavage planes to indeterminate depths. This should allow shrubs to better capitalize on deep, localized pockets of moisture. Unfortunately, such dynamics are rarely studied quantitatively because of the difficulty of measuring soil moisture budgets or root distributions under such conditions, but they are implicated by plant distribution patterns in many areas. Indeed, despite the visual austerity of such habitats, rooting into major joints and cracks in bedrock outcrops can create such a favorable microsite by concentration of runoff in localized areas that elevational limits of tree and shrub distributions may be substantially lowered as would be expected along riparian corridors or other unusually mesic habitats (Loope 1977). Even in deep soils, shrubs tend to have deeper root systems than grasses, but, in addition to this, shrubs may be more efficient than grasses at extracting deep water. Shrubs are sometimes able to draw on deep soil moisture to a greater extent than would be predicted from root biomass distribution alone (Sturges 1980), and this is due in part to an intriguing phenomenon reported by Richards and Caldwell (1987), and named by them "hydraulic lift." During the late spring and early summer most of the remaining soil moisture is present in deeper soil layers where rooting density may be relatively low. Due to low densities, deep roots alone may be unable to absorb water as quickly as it is lost by the transpiring shoot. During the night, water is actually redistributed within the soil, flowing from deep soil layers through the roots and back out into shallower soil layers. This is the phenomenon named "hydraulic lift," and the advantage to the plant is thought to be a reduction in the rooting density necessary to fully

exploit the resources of the deepest soil layers. During the day, rates of water movement from the soil into the roots can be limiting to shoot activity. Moistening the upper soil layers by nocturnal hydraulic lift increases the root surface area for absorption during the periods of high transpiration. Daytime water use can be supported by the entire root system and not just by the low-density deep roots (Caldwell and Richards 1989).

The root systems of Great Basin shrubs and Mojave Desert shrubs differ strongly in several ways. (1) Mojave Desert shrubs often have maximal rooting densities at soil depths of 0.1–0.3 m, and maximum root penetration of 0.4–0.5 m (Wallace et al. 1980). These shallower roots are due to lower rainfall and warmer winter temperatures resulting in shallower wetting fronts in the soil, and the development of shallow caliche layers. (2) Great Basin species have more roots in the shallowest 0.1 m soil layer (Wallace et al. 1980, Dobrowolski et al. 1990). Differences in soil temperatures have been used to explain these patterns, but the link between cause and effect is less obvious in this case, and conjectures should be viewed cautiously. Much hotter soil temperatures in the Mojave may be detrimental to roots in the uppermost few centimeters during summer, and the rapidly drying soil surface may be too ephemeral a moisture resource to favor large investments in roots. In contrast, snowmelt and cooler spring temperatures may result in less rapid evaporation from the soil surface in the Great Basin and thus favor more rooting by perennials in that zone. (3) Because of the greater soil volume exploited, as well as the high root density of Great Basin species, their ratios of root:shoot biomass are about twice that of Mojave Desert species (Bamberg et al. 1980, Dobrowolski et al. 1990).

ADAPTATION TO SALINITY.—When annual precipitation levels are much lower than potential evaporation, salts are not leached to any great depth, and they can accumulate within the root zone. This is especially important in association with particular bedrock outcrops, such as the Mancos and Chinle shales, which release high concentrations of salts during weathering (Potter et al. 1985). Precipitation increases with elevation, and, following major storms or spring snowmelt, there may be surface runoff and recharge of groundwater systems that transport water from high elevations into closed basins. Streams in the Great Basin usually terminate in evaporative pans where salinities reach extreme levels and salts precipitate forming a surface crust. The water table near these evaporative pans is often at or very near the surface throughout the year, but, if there is no groundwater flow out of the basin, it too is often quite saline (Dobrowolski et al. 1990). Salinities are lowest on slopes and at higher elevations where precipitation exceeds evaporative loss, and they increase on more level terrain and in lower-elevation basins where evaporation exceeds precipitation. Salinities may also be higher in areas where wind-borne materials are transported from saline playas to surrounding slopes (Young and Evans 1986). These patterns of soil salinity are important in determining plant distributions, with more specialized salt-tolerant species (halophytes) replacing less-tolerant species repeatedly along gradients of increasing salinity. In general, species diversity is low on saline soils. The vast majority of tolerant shrub species in our deserts, and all the shrubs specifically mentioned in this section, belong to a single plant family, the Chenopodiaceae (goosefoot family). Most other important taxa in the saline communities are grasses.

In the most extreme case of hypersaline salt flats and pans there may be standing water in the wet season with saturating salt concentrations. Under such conditions, only microflora consisting of a few species of photosynthetic flagellates, cyanobacteria, and halobacteria are commonly found. The halobacteria appear to be unique in having adapted in an obligate manner to the high salinities of these environments. They not only tolerate, but *require*, high cytoplasmic salinities for membrane stability and proper enzymatic function (Brown 1982). In strong contrast to this, algae and all higher plants growing in hyper-saline environments show severe inhibition of enzyme function at high salinity, and they must compartmentalize salt-sensitive metabolic processes in cellular regions of low ionic strength (Munns et al. 1982).

The best definition of a halophyte is simply a plant tolerant of soil salinities that would reduce the growth of unspecialized species. This is somewhat circular, and that reflects our limited understanding of how halophytes do what they do. Halophytes are more likely to use Na+ in their tissues for osmotic adjustment, while glycophytes are more likely to have high K+ (Hellebust 1976, Flowers et al. 1977), but there are numerous exceptions. Other differences

may be more quantitative than qualitative. Various aspects of mineral nutrition in halophytes are less sensitive to high soil salinities, but unique mechanisms to achieve this tolerance have rarely been identified. It is widely held that the ability to compartmentalize salts and restrict high Na+ concentrations to the vacuole is of crucial importance (Caldwell 1974, Flowers et al. 1977, Briens and Larher 1982). This conclusion is based primarily on indirect evidence of low enzyme tolerance of salinity, however, rather than direct measurements of actual salt compartmentalization (Munns et al. 1982, Jefferies and Rudmik 1984).

Halophytes differ in which ions reach high tissue concentrations when all plants are grown on the same medium (Caldwell 1974). Some will concentrate Cl−, for instance, while others concentrate SO_4^{-2}. These differences do not necessarily determine plant distributions, such as occurrence in soils dominated by NaCl versus $NaSO_4$, but rather seem to reflect different regulatory specializations in plant metabolism (Moore et al. 1972). A strong requirement for a unique composition of soil salts is the exception rather than the rule, and the most important effect of soil salinity seems to be a disruption of plant water relations from low soil osmotic potentials rather than toxic effects of specific ions. Halophytes tolerate these conditions by having better regulatory control over ion movement within the plant, ion compartmentalization at both tissue and subcellular levels, and better homeostasis of other aspects of mineral nutrition in the presence of very high Na+.

Salinity poses three major problems for higher plants. First, salts in the soil solution contribute an osmotic potential depressing the soil water potential, and this may be aggravated as salts become concentrated with soil drying. Even when substantial moisture is present, plant tissues must endure very low water potentials to take it up, and this requires a specialized metabolism. Second, any salts entering the plant with the transpiration stream will be left behind in the leaf intercellular fluids as water evaporates from the leaf. This can result in salt buildup in the intercellular solution causing water movement out of the cells and leading to cellular dehydration. Third, salts entering the cytoplasm in high concentration will disrupt enzyme function. Halophytes are able to deal with all of these factors over a wide range of soil salinities. Halophytes show a greater capacity

for osmotic adjustment, and positive photosynthetic rates can be measured in the leaves of many halophytes at leaf water potentials as low as −90 to −120 bars (Caldwell 1974), well below the range that would result in death of even desert-adapted glycophytes. This is accomplished in part by transforming the available salts in the environment into a resource and using them for osmotica in plant tissues (Moore et al. 1972, Bennert and Schmidt 1984). Many halophytes actually show stimulation of growth rates at moderate environmental salt levels.

Halophytes too must deal with the problem of salt buildup in the leaves, and they do so by a wide variety of processes. There is a great deal of interspecific variation in which method(s) are used. All the methods appear to incur substantial energetic costs associated with maintaining high ion concentration gradients across key membranes (Kramer 1983). Exclusion of salts at the root is possible; this is the method most employed by winterfat (*Ceratoides lanata*). Saltbush (*Atriplex* spp.) has specialized hair-bladders on the leaf surface into which excess salts are actively pumped. The hairs eventually rupture, excreting the salts to the outside. Other plants may transport salts back to the root via the phloem. Many plants exhibit increased leaf succulence when grown under high salinity, and this increase in cell volume can create a sink for salts within the leaf without raising salt concentrations or further lowering leaf osmotic potential.

In strong contrast to the evident importance of temperature and rainfall pattern in favoring C_3 versus C_4 grasses, C_4 shrubs tend to belong to edaphic communities associated with saline soils. The same species may occur in both warm and cold deserts, and in areas with both winter and summer rainfall patterns. This is an intriguing difference, but the physiological basis linking C_4 shrubs with high salinity is less well understood than the tradeoffs associated with temperature and controlling C_3 and C_4 grass distributions. Species number and percent cover by shrubs such as saltbush (*Atriplex* spp.) and inkweed (*Sueda* spp.), which possess the C_4 pathway, usually increase dramatically with increasing salinity on well-drained soils. In marshy habitats or soils with a shallow, saline water table, however, halophytic C_3 species such as pickleweeds (*Allenrolfia* spp. and *Salicornia* spp.) and greasewood (*Sarcobatus vermiculoides*) regain dominance. It has been suggested that higher water-use efficiency by C_4

species may be advantageous on saline soils to help avoid salt buildup in the leaf tissues. However, it has not been shown that transpiration rate is an important factor controlling salt buildup in the leaves of halophytes when compared with other regulatory mechanisms (Osmond et al. 1982), nor does this hypothesis explain the dominance of C_3 species in wet saline soils. In the greasewood and pickleweed communities, soil salinities are extreme, but soils remain wet throughout the growing season, or else groundwater is available within the rooting zone (Detling 1969, Hesla 1984). As a consequence, plant water potentials do not reach the extreme low values of the saltbush communities. Over a wide range of soil salinities, plants such as greasewood appear to draw on readily available deep soil moisture, and high leaf conductances are maintained throughout the summer (Hesla 1984, Romo and Haferkamp 1989). The highest whole-plant water-use rates may occur in the presence of high soil salinity in mid-summer (Hesla 1984). The communities in which C_4 shrubs are most prevalent have summer stress from both high soil salinity and mid-summer soil water depletion combined. These species reach much lower plant water potentials during summer than either nonsaline communities or wet-saline communities. The role of C_4 photosynthesis in tolerating these conditions remains to be determined, but it could be related to avoiding excessively low leaf water potentials either by (1) retarding soil moisture depletion, which both lowers the soil matrix potential and concentrates soil salts, or (2) avoiding exacerbation of low soil water potentials due to high flux rates and large water potential gradients between the leaf and root. Water movement in the xylem occurs under tension, and anatomical features that avoid cavitation in the xylem at extremely low water potentials usually reduce the hydraulic conductivity of the xylem per unit cross-sectional area (Davis et al. 1990, Sperry and Tyree 1990). Low specific conductivity of the xylem will, in turn, predispose the plant system to large water potential gradients between roots and shoots, causing an even greater depression of leaf water potential. This problem could be ameliorated either by increased cross-sectional area of the xylem by increased allocation to wood growth, or by features such as C_4 photosynthesis that reduce the flux rate of water associated with photosynthetic activity under warm conditions.

NUTRIENT RELATIONS

ACQUISITION OF MINERAL NUTRIENTS.—Apart from the very high elevation montane zones, water appears to be the most limiting resource in the Great Basin and Colorado Plateau communities. Productivity is usually well correlated with yearly fluctuations in precipitation and spring moisture recharge over a wide range of values (Daubenmire 1975, Kindschy 1982), and competitive success has more often been associated with soil water use patterns than nutrient budgets. Nonetheless, addition of mineral fertilizer sometimes does result in modest increases in productivity, and studies have shown strong effects of neighboring plants on nutrient uptake rates (Caldwell et al. 1987). These dynamics have been less studied than have plant water budgets, and broad ecological relationships are just now being worked out in detail. Nutrient acquisition has been shown to be a major factor determining community composition only in very special habitats such as large sand dunes (Bowers 1982) or unusual bedrock (DeLucia and Schlesinger 1990).

MICROPHYTIC CRUSTS.—Throughout the Great Basin and Colorado Plateau, it is common for the exposed soil surface to be covered by a complex community of nonvascular plants including dozens of species of algae, lichens, and mosses (West 1990). These organisms often form a biotic crust in the upper few centimeters of the soil and, when undisturbed, may result in a very convoluted microtopography of the surface. While a detailed discussion of the microphytic crusts is beyond the scope of this review, it is important to realize that percent cover by such crusts often exceeds that of the vascular plants, and their contribution to total ecosystem productivity is considerable. Perhaps most important to co-occurring vascular plants are the nutrient inputs to the soil by nitrogen-fixing crust organisms (cyanobacteria and lichens). These inputs will be particularly important in the cold desert where few vascular plants form symbiotic relationships with nitrogen-fixing bacteria.

NURSE PLANTS AND FERTILE ISLANDS.—In many desert areas, including both the Mojave and the Great Basin, establishment of new individuals may occur preferentially under the existing canopies of already established individuals. These previously established individuals may then be referred to as nurse plants. Preferential

establishment under nurse plants may occur in spite of the fact that 75% or more of the ground area may be bare interspaces between plant canopies. The phenomenon can be important in both steady-state community dynamics and also successional patterns following disturbance (Wallace and Romney 1980, Everett and Ward 1984). Two somewhat distinct factors contribute to the nurse-plant phenomenon. The first has to do the with beneficial effects of partial shading and reduced wind under existing canopies resulting in cooler temperatures and possibly moister soil conditions in the surface layers. These interactions depend directly on the presence of the nurse plant in creating a favorable microsite, and have been studied with particular reference to pinyon and juniper establishment in the Great Basin. A second factor involves the creation of fertile islands by the prolonged occupation of the same microsite by many generations of plants; this can make the fertile island a preferred site even if the previous occupant is already deceased. This microsite improvement occurs due to preferential litter accumulation and more extensive root growth directly under a plant canopy, and deposition of aeolian materials under reduced wind speeds in plant canopies. In time, soils under existing plants may come to be slightly raised above the interspace level, have a lighter, loamier texture, higher organic matter content and better soil structure, less surface compaction, better aeration and more rapid water infiltration, and/or higher levels of available mineral nutrients than immediately adjacent interspace soil (Vest 1962, Wood et al. 1978, Romney et al. 1980, Hesla 1984, West 1989, Dobrowolski et al. 1990). Direct effects of nurse plants and indirect effects of fertile islands should complement and reinforce each other in maintaining selective spacial patterns of seedling establishment. Surface soil under halophytes may also show increased salinity (Richard and Cline 1965) due to excretion of excess salts by the canopy or translocation and re-excretion from the roots.

DIVERSITY OF GROWTH FORMS

One of the striking features of the cold desert vegetation is the uniformly low stature of the vegetation. This is undoubtedly due to several factors, and few studies have specifically addressed the role of plant stature in these communities. Since low temperatures may limit photosynthesis in the cool spring, and earlier growth on limited soil moisture reserves may be competitively advantageous, occupying warm microsites may be favored. Substantial increases in air temperature and reductions in wind speed will exist in the lowest meter next to the ground, and especially in the lowest decimeter. Low cushion plants or low, dense shrub canopies should have warmer spring leaf temperatures by virtue of being short and by virtue of leafing out first in a dense clump of old dead leaves and twigs (Smith et al. 1983, Wilson et al. 1987). This advantage may be partially offset by overly high temperatures in summer for species remaining active all summer. Stature is also likely to affect aeolian deposit of materials under the shrub canopies (Wood et al. 1978, Young and Evans 1986), snow accumulation (Branson et al. 1981, West and Caldwell 1983), and the likelihood of winter desiccation under cold, windy conditions (Nelson and Tiernan 1983). All of these could be important factors, but few detailed studies have been done.

Having considered the relationships of the dominant plant habits and phenologies to climate, it is perhaps instructive to consider why some of the other famous desert life forms are so poorly represented in this region. Three life forms which are prominent features of the warm desert but inconspicuous elements of the cold desert are (1) large CAM succulents (e.g., cacti and agave), (2) opportunistic drought-deciduous shrubs specialized for rapid leaf-flushing, and (3) annuals. Definitive work explaining the structural uniformity of the vegetation is not available, but the environment is well enough understood to identify at least some of the likely causes.

CAM SUCCULENTS.—Most of the large CAM succulents are not tolerant of freezing temperatures, and most extant species would be excluded from the Great Basin by this factor alone. There are, however, a sufficient number of species which have adapted to tolerate cold temperatures that we are justified in asking why they have not undergone more adaptive radiation, or claimed a more prominent role in these communities. The most important factor limiting this life form is probably the importance of the cool spring growing season. CAM succulents generally (1) allocate very little biomass to root (root/shoot ca. 0.1), (2) are shallow rooted, (3) store moderate-sized (compared to soil water-holding capacity) water reserves inside

their tissues when water is available in the surface soil layers, and (4) use their stored water in photosynthesis with unparalleled water-use efficiency by opening their stomata only at night when temperatures are cool (Nobel 1988). They are favored by (1) very warm days (30–40 C), which allow them to have higher photosynthetic rates and cause competing species to have very low water-use efficiencies; (2) large diurnal temperature fluctuations allowing for cool nights (10–20 C) which allow them to have high rates of CO_2 uptake with high water-use efficiency; and (3) intermittent rainfall, which only wets the upper soil layers so that the limitations of their shallow roots and water-hoarding strategy are compensated for by the ephemeral nature of the soil water resource. These conditions are somewhat poorly met in the cold desert. The important water resource is one of deep soil recharge that favors deep-rooted species and confers much less advantage on internal water hoarding. Freezing tolerance in CAM succulents appears to be associated with low tissue water contents, and this may inhibit uptake of water when it is plentiful in the surface layers in the thermally vacillating early spring (Littlejohn and Williams 1983). Furthermore, water-use efficiencies of C_3 and C_4 species are quite high in the cool spring.

Nonetheless, even moderate amounts of summer rain in the southern and eastern portions of the Great Basin result in numerous species of cacti. Due to the open nature of the understory, many of these species have a large elevational range, and they are often more common in the pinyon-juniper or even the montane zone than on the desert piedmont slopes. Almost all of these cacti are small, usually 5–20 cm high, with a small, globose (e.g., *Pediocactus simpsonii*), prostrate (e.g., *Opuntia polycantha*), or low, caespitose habit (e.g., *Echinocereus triglochidiatus*). This allows them to take advantage of the warmer daytime temperatures near the ground in the spring and facilitates an insulating snowcover during the coldest winter periods. The number of and total cover by cacti increase considerably with increased summer rainfall on the Colorado Plateau, but only in the eastern Mojave with both summer rain and warm spring temperatures do we find the larger barrel-cactus (e.g., *Ferocactus acanthoides*) and tall, shrubby chollas (e.g., *Opuntia acanthocarpa*).

OPPORTUNISTIC DROUGHT-DECIDUOUS / MULTIPLE LEAF-FLUSHING SPECIES.—This habit, like that of the succulents, is favored by (1) intermittent rainfall wetting only shallower soil layers, and (2) warm temperatures allowing for rapid leaf expansion in response to renewed soil moisture. Again, these requirements are not well met in the Great Basin. The primary moisture resource is a single, deep recharge in the winter. Most shrub species are deep rooted, and rather than experiencing vacillating water availability, they have active root growth shifting to deeper and deeper soil layers during the season, thus producing a gradual and continuous change in plant water status. This allows many spring-active shrubs to remain partially evergreen throughout the summer, and, in regions where it occurs, they are able to make rapid use of any moisture available from summer precipitation without the need for renewed leaf production. The only shrub reported to have multiple leaf flushes in response to late spring or summer rain in the Great Basin is the diminutive and shallow-rooted *Artemisia spinescens* (Everett et al. 1980). Some species found in the Great Basin are reported to have multiple growth cycles/year where they occur in the Mojave (Ackerman et al. 1980).

ANNUALS AND LIFE-HISTORY DIVERSITY.— The spectacular wildflower shows displayed in favorable years in the Mojave Desert do not occur in the cold desert of the Great Basin (Ludwig et al. 1988). Annual species are few in number, and, except in early succession after fire in woodlands or on very disturbed sites, they rarely constitute a major fraction of total community biomass. This is undoubtedly related to several complex factors, but various aspects of precipitation patterns are likely to be among the most important. To begin with, the paucity of summer rain in some parts of the Great Basin may largely eliminate an entire class of C_4 summer annuals important in the floras of other regions including the Colorado Plateau. Other aspects than seasonality are also crucial, however. Very low means of annual precipitation are commonly associated with large annual floras, but correlated with low mean precipitation is high year-to-year variation in precipitation which some authors have argued is equally important. The coefficient of variation (CV) in precipitation shows a relationship to mean precipitation in the Great Basin and Colorado Plateau (Fig. 2) very similar to that found in warm
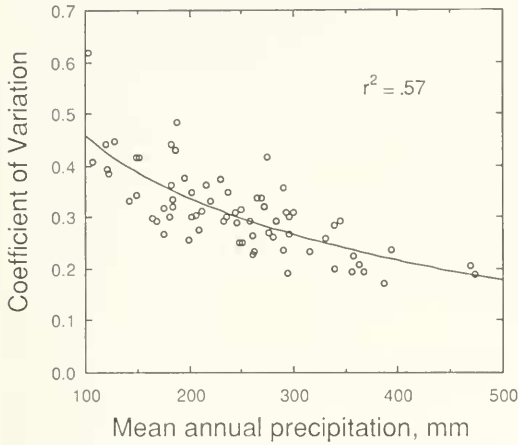
Fig. 2. The relationship between mean precipitation and the variability of rainfall between years as measured by the coefficient of variation in annual precipitation. The data include points scattered throughout the Great Basin in Utah and Nevada and the Colorado Plateau in Utah and Arizona. The line shown is the least squares best fit for the data: CV = 1.27 − 0.403 ° log(mean annual precipitation, mm) (n = 69 sites, $p < .001$).
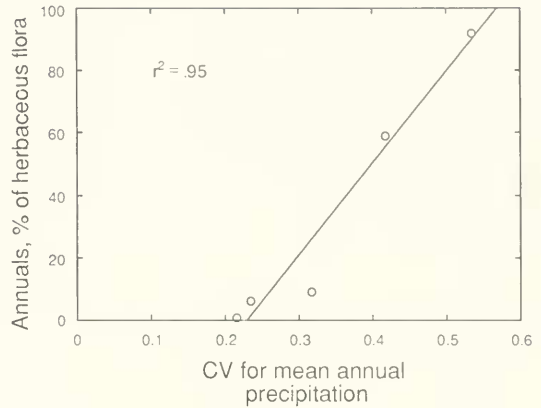
Fig. 3. The relationship between reliability of annual precipitation and life-history strategy of herbaceous plants. The site with greatest representation of annuals is Death Valley in the Mojave Desert, the second highest is Canyonlands in the Colorado Plateau of southeastern Utah, and the other three sites are Great Basin Cold Desert or shrubsteppe (data were collected by Kim Harper and previously published in Schaffer and Gadgil 1975).

deserts (Ehleringer 1985). Although mean precipitation has the greatest single effect, there are, additionally, important geographic influences on the CV of precipitation which are independent of mean precipitation. A multiple regression of the CV of precipitation on log(mean annual precipitation), latitude, and elevation in the Great Basin has an r^2 of .81 and indicates that each variable in the model is highly significant ($p < .001$ or better). For a given mean precipitation, the CV increases with decreasing altitude in the Great Basin, but an independent effect of elevation was not significant in the Colorado Plateau. The CV also increases from north to south in the Great Basin and increases from south to north in the Colorado Plateau, which results in a latitudinal band of greatest annual variability running through southern Nevada and Utah. This band is related to two major aspects of regional climate. Moving southward in the Great Basin, temperatures gradually increase, favoring moister air masses and more intense storms, but sites are more removed from the most common winter storm tracks, and the number of rainy days per year decreases (Houghton 1969). Moving northward from Arizona and New Mexico, the southern Nevada and Utah band of highest precipitation variability also corresponds to the northernmost extent of summer storms associated with the

Arizona monsoon, and the region where the fraction of summer rain increases substantially moving southward. This zone also has some of the most arid sites of the entire region located along the transition to the Mojave Desert in southern Nevada and the canyon country of southeastern Utah, and these sites can be expected to have the highest variability due to both low mean rainfall and geographic position correlated with regional weather patterns. Because the Great Basin and Colorado Plateau are only semiarid, the CV of annual precipitation is not usually as high as in many of the more arid warm deserts (Beatley 1975, Ehleringer 1985), but particular sites may be both arid and highly unpredictable.

Harper (cited in Schaffer and Gadgil 1975) found that the prevalence of annuals was positively associated with the CV in annual precipitation for five sites located in the Great Basin, Colorado Plateau, and Mojave Desert (Fig. 3). The largest annual populations occurred in Death Valley (Mojave), followed by Canyonlands (Colorado Plateau in southeastern Utah). One interpretation of this relationship is that high variability in total precipitation between years may be associated with high rates of mortality and therefore favor early reproduction and an annual habit (Schaffer and Gadgil 1975). Many desert annuals are facultatively perennial in better-than-average years, and some have

perennial races or sister species (Ehleringer 1985). The dynamics and distributions of these closely related annual and perennial taxa should receive further study in regard to their expected life span, reproductive output, and relationships to climatic predictability. Another perspective is to ask how competition between very distinct shrub and annual species is affected by precipitation variability. While in many respects complementary with the optimal life history arguments, this approach emphasizes how large differences in habit affect resource capture and competition rather than focusing on subtler differences in mortality and reproductive schedules. The lower variability of precipitation in much of the Great Basin compared to the Mojave and Sonoran deserts, as well as the more reliable accumulation of moisture during the winter-recharge season, may favor both stable demographic patterns and growth of perennials. Annuals tend to be shallow rooted (most roots in upper 0.1 m depth), and they are poorly equipped to compete with shrubs for deep soil moisture. If shrub density is high, and years of unusually high mortality are rare, then shrubs may largely preempt the critical water and mineral resources and suppress growth of annuals. The dominant shrubs of the warm deserts do not have high root densities in the upper 10 cm of the soil profile (Wallace et al. 1980), have lower total root densities, and have lower total cover when compared with Great Basin perennials. Annuals are therefore likely to experience more intense competition from shrubs in the Great Basin. This conjecture is further supported by considering that perennials in the Great Basin generally transpire 50% or more of the annual moisture input over a wide range of yearly variations. In the Mojave this fraction may average only 27% and vary between years from 15 to 50% at the same site (Lane et al. 1984), or even be as low as 7% (Sammis and Gay 1979). The reduced overlap in rooting profiles and the greater availability of unused moisture resources may have favored the development of annual floras in the Mojave Desert more than in the Great Basin. With severe disturbance from grazing and other anthropogenic activities, exotic annual species have invaded many Great Basin communities. Once established following disturbance, these annuals are not always easily displaced by short-term shrub succession. While this discussion has been presented in the context of annuals versus perennials, tradeoffs between short- and long-lived perennials may be influenced by very similar climatic parameters, sometimes operating over different time scales.

Other factors that may be important in the ecology of Great Basin annuals include the effects of the very well developed cryptogam soil crusts or vesicular horizons on seed predation (ability of seeds to find safe sites), seed germination, and seedling establishment. The restriction of winter growth by cold temperatures could also be of crucial importance, inhibiting the prolonged establishment period enjoyed by winter annuals in warm deserts. Fall germination followed by low levels of photosynthesis throughout the mild winter is essential for vigorous spring growth of winter annuals in the Mojave, and, while heavy spring rains may cause germination, such late cohorts rarely reach maturity (Beatley 1974). Annuals are common in transition zone sites of the ecotone between Mojave Desert and Great Basin plant communities in southern Nevada, but associated with changes in perennial species composition along decreasing mean temperature gradients in that region are decreases in annual abundance (Beatley 1975).

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